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Studies in Morphogenesis, III.

On the

Acclimatization of Organisms to High Temperatures.

By

C. B. Davenport and W. E. Castle.

Separat-Abdruck

aus dem

Archiv für Entwicklungsmechanik der Organismen,

II. Band, 2. Heft.

Leipzig

Wilhelm Engelmann

1895.

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On the

Acclimatization of Organisms to High Temperatures¹⁾

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Eingegangen am 4. März 1895.

The significance of the phenomena of acclimatization to morphogenesis has not heretofore been sufficiently appreciated. It becomes apparent, however, when we recognize that the morphogenic process is a series of responses to stimuli²⁾.

Now what the response of protoplasm to any stimulus shall be depends upon the qualities of the protoplasm as well as the nature of the stimulus, for the same stimulus awakens unlike responses in different protoplasms, and from this results, in part, the unlikeness in development of different species. And when we come to inquire wherefore various protoplasms are unlike in their responsiveness, we must conclude that one of the causes of unlikeness is the dissimilar experiences which the protoplasms of different species have undergone, for we can make dissimilar in responsiveness protoplasms which were originally alike by subjecting them to diverse experiences. This is seen in the phenomenon of acclimatization of organisms.

Acclimatization of organisms may be defined as the phenomenon of increased resistance capacity acquired by them, and may be divided into two classes: race acclimatization, and individual acclimatization. In the latter the resistance is acquired during its

¹⁾ Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College. E. L. MARK, Director. No. XLVI.

²⁾ Compare on this subject the excellent paper of HERBST. 1894. Biol. Centralbl. XIV. pag. 756—771; 800—807.

lifetime by the individual when subjected to the action of an untoward environment.

In the present paper we propose to discuss individual acclimatization to high temperatures.

In considering this subject we shall speak, first of the recorded cases of organisms having become acclimated in nature to high temperature; secondly, of the experimental work which has been done in producing individual acclimatization; and, lastly, of the changes which protoplasm must undergo in individual acclimatization.

a) The Acclimatization of Organisms to High Temperatures in Nature.

For every individual there is, as is well known, an optimum temperature for its activities. As we elevate the temperature above this, we eventually reach a point where motion, after having somewhat diminished, suddenly ceases, producing what is known as "heat rigor", a condition from which the organism will return to activity upon lowering the temperature. A few degrees above the heat rigor point is that of death.

As an introduction to the consideration of the acclimatization of organisms to high temperatures, we tabulate the results of experiments by numerous observers whereby the maximum temperatures of numerous organisms, under what may be called otherwise normal conditions, have been determined.

Table I.

Results of experiments to determine the maximum temperature of organisms in water, or the highest temperature which organisms reared under normal conditions will withstand.

Species	Max. temp.	Conditions of Experiment	Authority
Bacteria	45—70°C.	Maximum temp. of growth in liquid	COHN, '77, pag. 253; '94, pag. 150.
Yeast	53°	Moist; average maximum	SCHÜTZENBERGER, '79, pag. 162.
Oscillatoriae	45°	Death point	DE VRIES, '70, pag. 388.
Spirogyra	44°	- -	DE VRIES, '70, pag. 388.
Oedogonium			
Cladophora	45—60°	- -	SACHS, '64, pag. 5.

Table I continued.

Species	Max. temp.	Conditions of Experiment	Authority
Various plant cells	47—48°C.	Died, with apparent coagulation	SCHULTZE, '63, pag. 49.
Aethalium sept.	40°	Plasmodium died after two minutes	KÜHNE, '64, pag. 87.
Protozoa.			
Amoeba	40—45°	Death point	KÜHNE, '64, pag. 46.
Actinophrys	42°	Death point. Activity lost at 38°	SCHULTZE, '63, pag. 32.
Various flagellata and swarm spores	40—60°	45—60° most usual. Heat rigor usually occurs between 40—50° and is lower for marine than for f. w. species. These temps. for the motile stage	BÜTSCHLI, '84, pag. 860. — STRASSBURGER, '78, pag. 611. — DALLINGER, '80, pag. 10.
Stentor	44—50°	Heatrigor point, temperature raised gradually	W. E. CASTLE (unpublished observation).
Vorticellidae	41—42°		SCHULTZE, '63, pag. 49.
-	45°	Can withstand only a short time	SCHÜRMAYER, '90, pag. 42.
Coelenterata.			
Actinia	38°	Gradually raised (1 hr.)	FRENZEL, '85, pag. 464.
Beroe ovatus	40°	Death point, suddenly subjected	VARIGNY, '87, pag. 63.
Mollusca.			
Various Mollusca	30—40°	Suddenly immersed	FRENZEL, '85, pag. 461—66.
Pleurobranchae	33°	Temp. gradually raised	- - -
Aplysia	33°	Died in three hours	- - -
Eledone	35°	Died	- - -
Young squids	37°	Heat rigor; died at 41°	BERT, '67, pag. 135.
Vermes.			
Turbellaria	44.5°	Death point	SCHULTZE, '63, pag. 49.
Anguillulidae	44.5°	- -	SPALLANZANI, 1777, pag. 56.
Rotifera	45—48° 98°	Moist	DOYÈRE, '42, pag. 29.
Tardigrada		Dried	BROCA, '61, pag. 44—46.
Diopatra	40°	Suddenly immersed, died quickly; at 30° lived indefinitely	FRENZEL, '85, pag. 461—65.

Table I continued.

Species	Max. temp.	Conditions of Experiment	Authority	
Terebella	27—30°C.	Suddenly heated; slowly warmed resisted 30°	FRENZEL, '85, pag. 461—65.	
"Bloodsucker"	44°	Death point	SPALLANZANI, 1777, pag. 56.	
Crustacea.				
Branchionus	47—48°	Death point	SCHULTZE, '63, pag. 49.	
Daphnia sema	33.5°	- -	PLATEAU, '72, pag. 316.	
Cyclops quadricor- nis	36°	- -	- -	
Cypris fusca		- -	- -	
Cypris sp.	47—48°	- -	SCHULTZE, '63, pag. 49.	
Gammarus rüselii	36°	- -	PLATEAU, '72, pag. 316.	
Asellus aquat.	43.5°	- -	- -	
Palaemon	26°	- - (suddenly sub- jected)	FRENZEL, '85, pag. 463.	
Scyllaris	30—40°	- -	- -	
Pagurus prideauxii	36°	Death point	DE VARIGNY, '87, pag. 173.	
Dromia vulgaris	38°			
Pisa gibbosa	36°			
Portunus puber.	34°			
Carcinus sp.	38°			
Grapsus sp.	38°			
Arachnida.				
Argyroneta aquat.	38.5°	Suddenly submerged	PLATEAU, '72, pag. 316.	
Hydrachna cruenta	46.2°	Submerged (?)	- -	
Insecta.				
Podura	27°	Suddenly subjected; died slowly. At 36° died at once	NICOLET, '42, pag. 11.	
Agabus bipustulat.	38°	Death point	PLATEAU, '72, pag. 316.	
Hydacticus trans- vers.	39°			
Culex pipiens, larva	40°			
Hydrous caraboides	42°			
Hydroporus dor- salis	42°			
Nepa cinerea	44—45°			-
Notonecta glauca				
Cloë diptera, larva				

Table I concluded.

Species	Max. temp.	Conditions of Experiment	Authority
Musca vom. (?)	37.5° C.	Death point	SPALLANZANI, 1777, pag. 56—58.
- - , larva	42.5°		
- - pupa	43.7°		
Silk worm larva	42.5°		
"Butterfly" larva	42.5°		
Culex larva	43.5°		
Echinodermata.			
Antedon	30°	Died rapidly	FRENZEL, '85, pag. 460—63.
Holothuria	30—40°	Death point	- -
Vertebrata.			
Many freshwater fishes	40°	Survived only a few seconds	EDWARDS, '24, pag. 114.
Fish	33°	Temp. elevated gradually	BERT, '76, pag. 169.
-	27—38°		DAVY, '63, pag. 125.
Hippocampus	30°	Lived half an hour	FRENZEL, '85, pag. 462.
Salamander	44°	Death point	SPALLANZANI, 1777, pag. 56.
Frog	40—42°	Suddenly subjected in water; death at once	EDWARDS, '24, pag. 374.
- adult	43.8°		SPALLANZANI, 1777, pag. 55.
- embryos	50—56°		OBERNIER, '66, pag. 22.
Rabbit	44—45°	Death point when raised gradually; convulsions at 42°	
Dog			
Man	45°	In water; giddiness in a few seconds	EDWARDS, '24, pag. 374.
Vertebrate muscle	40—50°		KÜHNE, '59, pag. 784—804.

Some authors (cf. PLATEAU, '72, pag. 317—319) seem to assume that there must be a temperature, approximately the same for all protoplasmic structures, at which death or heat rigor will occur. The above list of cases, in which the death point has been determined for organisms of every group of the Animal Kingdom does not seem to bear out the assumption.

In considering the results, however, one must remember that they have been attained under diverse conditions. Such differing conditions are known to give results which cannot be directly compared. Thus individuals of the same species will die at dif-

ferent temperatures according as they are suddenly subjected to the high temperature, or gradually accustomed to it. Also, a lower temperature, long continued, often produces the same result as a higher temperature during a brief period. Unless otherwise stated the conditions are, in most cases, gradual subjection continued for a short time only. The quality of the water in which the organisms are living is supposed to be, except for its temperature, normal for the species.

Summarizing Table I, we find:

The Protista have the highest maximum temperature of any group, it being about 60° for active organisms in water. The Ciliata, however, show the decidedly low maximum of 42° . Among the Metazoa, the highest maxima recorded are $44-45^{\circ}$ for some insects (PLATEAU); viz., *Nepa* (water-scorpion), *Notonecta* (water-boatman), and *Cloë* larva; and 46° for *Hydrachna* (water-mite), none of which forms can, properly speaking, be called submerged. Other animals reaching over 40° C. are certain fresh-water worms (SCHULTZE), 44.5° , *Asellus aquaticus*, 43.5° , and *Hydroporus dorsalis* (a water beetle, not submerged), 42° .

For the great majority of Metazoa whose maximum temperature has been determined, this lies between 30° and 40° C. Of animals dying at or below 30° there are few examples and these are mostly cases of sudden transference from cool to hot water. Thus *Antedon* and *Hippocampus* died at about 30° and *Terebella* between 27° and 30° C.

One may, accordingly, say in conclusion that Metazoa can not under ordinary circumstances live continuously at over 45° , and that they usually do not reach over 40° C.

This lower temperature is probably the true maximum in many cases where a higher limit is given, for too little care has been exercised in most cases to determine the temperature of the water immediately upon, and for a few minutes after placing the animals in the water, — an operation which lowers the temperature.

Although under ordinary circumstances Metazoa will not live at a temperature above 45° , and 60° is the highest temperature which Protista, taken from ordinary waters, will withstand, it has long been known that organisms live in certain hot springs in waters of considerably higher temperature.

We here tabulate the more important of these cases:

Table II.

List of species found in hot springs, with the temperatures and localities at which they occur.

Species	Temp. C.	Locality and Conditions of life	Authority
<i>Chroococcus</i> <i>Protococcus</i> or <i>Nostocs</i>	51—57° 90°	Benton's Hot Springs, California Geysers, Lake Co., Cal.; not abundant at this tempera- ture	WOOD, '74, pag. 34. BREWER, '66, pag. 391; also WYMAN, '67, pag. 155.
<i>Nostocs</i> <i>Anabaena thermalis</i>	51—57° 57°	Benton's Hot Springs, Cal. Dax, warm springs	WOOD, '74, pag. 34. SERRES, '80, pag. 13—23.
<i>Leptothrix</i> <i>Oscillaria</i> - - - - - - -	44—54° 54—68° 57° 60—65° 60—65° 75.5° 81—85° 98° ²⁾ 73°	Carlsbad Springs Yellowstone Nat. Park, U.S.A. Algeria, Constantine pro- vince, waters of Hammam- Meskhoutin Geysers, Lake Co., California Hot Springs, Arkansas, U. S. A. (LONG) Himalayan Hot Springs Ischia ¹⁾ Iceland, water of hot spring Outlet of Lake Furnas, Azores	COHN, '62, pag. 539. WEED, '69, pag. 399. GERVAIS, '49, pag. 11. BREWER, '66, pag. 392. JAMES, '23, II, pag. 291. HOOKER, J. D., '55, pag. 24. EHRENBERG, '59, pag. 493. HOOKER, W., '13, pag. 161. DYER, '74, pag. 326; cf. MOSLEY, '74, pag. 324.
Diatoms		Frequently associated with the lowest algae in hot springs	
<i>Physa acuta</i> ⁴⁾	33—35°	Sources of Dax, St. Pierre, France	DUBALEN, '73, pag. iv.
<i>Paludina</i> sp.	50°	Thermal waters, Abano, Pa- dua	DEBLAINVILLE, '24, pag. 141.

¹⁾ HOPPE-SEYLER ('75, pag. 119, 120) who examined Ischia, found no algae living at a temperature much above 60° C.

²⁾ This temp. of the hot spring taken from FLOURENS, '46, pag. 934.

³⁾ "In water so hot that the finger could be borne in it only for a short time." Probably "about 149 to 158° F." (65 to 70° C.) MOSLEY, '74, pag. 324.

⁴⁾ "Various species of *Pisidium*, *Sphaerium*, *Limnaea*, *Planorbis*, and of the *Ammicolidae* occur in waters of thermal springs of high temperatures." DALL, '92, pag. 12.

Table II concluded.

Species	Temp.C.	Locality and Conditions of life	Authority
"Bivalve testaceous animal"	? ¹⁾	Hot Springs, Arkansas	MITCHILL, '06, pag. 306 ?.
Rotifera and Anguillulidae	31—44 ⁰	Carlsbad Springs, Bohemia	COHN, '62, pag. 539.
Anguillulidae	45 ⁰	Aix, Springs	DE SAUSSURE, 1796, pag. 13, § 1168.
-	81 ⁰	Ischia, in hot springs	EHRENBERG, '59, pag. 494.
Cypris balnearia	45—50.5 ⁰	Hamam-Meskhoutin	MONIEZ, '93, pag. 140.
Stratiomys larva	69 ⁰	In hot spring, Gunnison Co., Colorado ³⁾	GRIFFITH, '82, pag. 599.
"A water beetle"	44.4 ⁰	In warm spring, India; abundant	HOOKE, J. D., '55, pag. 24.
"Water beetle"	? ⁴⁾	Hot Spring, Port Moller, Alaska	DALL, W. H. (personal letter).
"Little insects"	? ⁵⁾	Hot Springs, Arkansas	JAMES, '23, II, pag. 291.
Fish ⁶⁾	86 ⁰	Lake on Isle of Lucon, Philippines	SONNERAT. 1774. pag. 206.
Sparus desfontain.	75 ⁰	Tozer and Cafra, Tunis, hot springs	SEMPER, '81, pag. 428.
Barbels	34 ⁰	?	BERT, '77, pag. 169.
Frogs	46 ⁰	"Baths of the Pise"	SPALLANZANI, 1777, pag. 55.

To summarize: Protista are stated to have been found in nature in waters at temperatures far above 60° C. Green algae appear to be the least resistant, for the highest temperature in which they have been recorded to live is 70° (MOSLEY). Bluegreen algae and allies withstand still higher temperatures; certainly above 80°, probably even to the boiling point of water. Metazoa are stated to live in natural waters at temperatures considerably

¹⁾ Too hot for the hand to bear.

²⁾ WYMAN ('67, pag. 154) seems inadvertently to have ascribed this statement to LONG (cf. JAMES, '23, II, pag. 291).

³⁾ The larvae were attached to the rock by one end.

⁴⁾ "Too hot for the hand to bear more than a moment or two."

⁵⁾ The "insects" were about the bottoms and sides of the hottest of the Arkansas springs.

⁶⁾ This statement can hardly be considered to be satisfactorily established.

above 45° C. Thus Mollusca live certainly at a temperature of 50° C., and probably higher, and Rotifera may withstand even 80° C.

Some of these temperatures, especially for Metazoa in water, seem almost incredible in the absence of great precision in the observations. Sources of error are numerous especially in determining the precise temperature of the stratum of water immediately surrounding the organism observed; for in some warm springs or their outlets the surface water is said to be much warmer than the deeper layers in which the organisms are found. In such unusual matters, moreover, the testimony of several independent and well-trained observers is desirable.

This much, however, seems perfectly well established: Organisms may live in hot springs at a temperature far above the highest which their allies, taken directly from ordinary water, can resist.

b) Experiments to Produce Individual Acclimatization.

No one doubts that in all the cases cited above the individuals living in hot springs have been derived from ancestors which lived in water whose temperature rarely exceeded 40° C. The race has therefore become acclimatized, and the question arises: How has that acclimatization been effected?

Now experiments have shown that organisms, when gradually accustomed thereto, may resist a temperature which would have killed them if they had been suddenly subjected to it. Therefore it seems probable that the acclimatization of organisms to hot springs has been a slow, long-continued process, during which they have become gradually accustomed to higher and higher temperatures, probably attaining the hot springs by slowly advancing up their effluent streams.

This adaptation may have taken place without selection, purely by the capacity of individual adaptation which organisms possess.

That individual adaptation is sufficient to account for the vitality of organisms in hot springs has been shown by experiment. The first series of experiments which we shall cite is that published by DALLINGER ('87), which illustrates individual adaptation to high temperatures in Protozoa; the second series of experiments has been made by ourselves, and evinces the capacity of individual adaptation in Metazoa.

The remarkable experiments of DALLINGER are not widely enough known. He kept Flagellata in a warm oven for many months.

Beginning with a temperature of 15.6°C ., he employed the first four months in raising the temperature 5.5° ; this, however, was not necessary, since the rise to 21° can be made rapidly, but for success in higher temperatures it is best to proceed slowly from the beginning. When the temperature had been raised to 23° , the organisms began dying, but soon ceased, and after two months, the temperature was raised half a degree more, and eventually to 25.5° . Here the organisms began to succumb again, and it was necessary repeatedly to lower the temperature slightly, and then to advance it to 25.5° , until, after several weeks, unfavorable appearances ceased. For eight months the temperature could not be raised from this stationary point a quarter of a degree without unfavorable appearances. During several years, proceeding by slow stages, DALLINGER succeeded in rearing the organisms up to a temperature of 70°C ., at which the experiment was ended by an accident.

It will thus be seen that by gradual elevation of the temperature Flagellata may be acclimated to a temperature of water far above that which they can withstand when taken directly from out of doors, and approaching that of the hottest springs containing life.

In this case it is plain that the high temperature acted upon the same protoplasm at the end of the experiment as it did at the beginning. But while the protoplasm at the beginning of the experiment was killed at 23°C ., at the end it withstood 70° .

The second series of experiments which we shall detail was performed on tadpoles by ourselves. Recently laid eggs of *Bufo lentiginosus* were used. Some were kept in water at a constant temperature of $24\text{--}25^{\circ}\text{C}$. (temperature of the water itself, not of the constant temperature apparatus), others at about 15°C . The individuals in both lots developed normally, though the former much more rapidly. At the end of four weeks the point of heat rigor was ascertained for each lot. To determine this, one or more tadpoles from each lot were put, in a small glass vessel, over a water-bath at $65\text{--}70^{\circ}\text{C}$. A thermometer was thrust into the water of the vessel, and as the temperature gradually rose the tadpoles were carefully observed. The point of heat rigor, 40° to 44° , was reached in about five or ten minutes. As soon as the tadpole was seen to be completely in a state of rigor, so that it would not move when poked sharply about the dish with a stick, the dish containing it was immediately removed from the water-bath, and either

set down on the table to cool, — in which case the entry "cooled slowly", or no entry, is made, — or was placed in a shallow dish of cold water, in which case the entry "cooled rapidly" is made. The water was usually cooled to about 30° .

If in any case a temperature was reached higher than that at which rigor occurred, that higher temperature is also recorded.

Following is a detailed account of the experiments performed between the latter part of April and the middle of June, 1894:

Series I.

Control. Tadpoles reared under natural conditions in pond at Botanic Gardens, temperature 15° . Taken May 25th. Experimented with on the same day (probably about four weeks old):

No. 1. One large individual: Heat rigor at 40° ; revived at 38.5° ; rigor, second time, 38° ; revived at 37.5° .

No. 2. One small individual: Heat rigor at 40° ; revived at 38.5° ; rigor, second time, 35° ; raised temperature to 38° ; temperature lowered, did not revive.

No. 3. Two medium sized individuals: Heat rigor at 40° ; revived on cooling.

No. 4. One medium sized individual and one large individual: Heat rigor, 40° ; cooled slowly; medium sized one revived at 35° ; large one did not revive.

No. 5. Two medium sized individuals: Heat rigor at 41° ; did not revive.

No. 6. Two medium sized individuals: Heat rigor at 40° ; did not revive.

Of the ten individuals, the extremes of temperature at which heat rigor occurred were 40° and 41° . The mean was approximately 40.5° .

Series II.

Control. One tadpole weeks old brought from the Botanic Garden was kept twelve days at between 16° and 20° , and went into heat rigor at 40° .

Series III.

Control. Two tadpoles reared from the egg, for four weeks at 15° .

No. 1. Heat rigor at 40° ; revived at 38° ; cooled to 25° ; heat rigor, second time, 39.5° ; revived on cooling; heat rigor, third time, 38.5° ; revived on cooling; heat rigor, fourth time, 37° ; moved faintly again at 35° .

No. 2. Heat rigor at 40°; cooled; heat rigor, second time, 38.5°; cooled; heat rigor, third time, 37°; did not revive on cooling.

Series IV.

Control. Reared at 15° for four weeks and two days.

No. 1. Heat rigor at 40; raised to 42°; cooled rapidly, but did not revive.

No. 2. Heat rigor at 39.5°; raised to 41.5°; cooled rapidly, but did not revive.

The mean temperature at which heat rigor took place for the first time in these control experiments on fifteen individuals is about 40.3°; extremes, 39.5° and 41°.

Series V.

Tadpoles reared from the egg in warm chamber at temperature of 24—25°. Three individuals, four weeks old, same age as in Series III.

Nos. 1 and 2. Heat rigor, 43.8°; did not revive when the temperature was lowered slowly.

No. 3. Put first into water at 10° for ten minutes; then into water at 35° over the water bath; heat rigor at 43°; revived on rapidly cooling; heat rigor, second time, 43°; revived on cooling; heat rigor, third time, 43°; cooled, reviving at 39°.

The mean temperature of heat rigor on first trial was for these three cases 43.5°; extremes 43° and 43.8°. Increase of temperature of heat rigor over control experiments 3.2°, which, we believe, indicates the effect of the adaptation to heat.

The remaining experiments are of interest, also:

Series VI.

Two individuals of preceding lot, reared for four weeks at 25—26° C., then for five days at 33—34°.

No. 1. Large individual; heat rigor at 43°; raised to 43.5°; cooled rapidly; revived at 38°; heat rigor, second time, 43°; raised to 43.8°; cooled rapidly, and revived; heat rigor, third time, at 44°; raised to 45°; revived slightly on cooling (moved tail faintly).

No. 2. Medium sized individual; heat rigor at 43°; raised to 43.8°; cooled rapidly, and revived; heat rigor, second time, 40°; raised to 45°; but did not revive.

Series VII.

One individual reared at 15° for four weeks, then brought gradually to 33°, where it was kept for two hours: Heat rigor at 38.5°; cooled rapidly, revived; heat rigor, second time, 37°. The comparatively rapid rise from 15° to 33° diminished rather than increased the capacity of resistance.

These experiments show that the capacity of toad tadpoles for resisting high temperatures may be increased in even so short a time as four weeks. Thus, when they are reared at a temperature of about 15° C., every tadpole goes into heat rigor at 41° C., or below; whereas, when they are reared at 24—25°, a temperature ten degrees higher, no tadpole dies under 43°, the average increase of resistance being 3.2°. This increased capacity of resistance is not produced by the dying off of the less resistant individuals for no deaths occurred in these experiments during the gradual elevation of the temperatures in the cultures. The increased resistance is due, therefore, to a change in the protoplasm of the individuals. The question now arises: In how far is this change in the protoplasm permanent? Will a return of the individual to cool water cause a return to the old point of heat rigor? We have made a few experiments on this subject.

Series VIII.

The tadpoles for these experiments were from the same lot as those employed in Series VI. They had been raised from the egg for twenty-eight days in water at 25—26° C., and for five days more at 33—34°. They were now kept for seventeen days in water at 15°. Four individuals were experimented upon.

No. 1. A very small individual; heat rigor occurred at 41°; cooled rapidly, revived; rigor again 41°; cooled rapidly, revived; rigor a third time at 38.5°; cooled rapidly, revived.

No. 2, a small individual, and No. 3, a large one, were treated together; No. 2 went into heat rigor at 42°; No. 3, at 41.5°; cooled rapidly; No. 2 only revived.

No. 4. Very large and active; rigor at 42°; cooled rapidly, revived.

The mean of these four trials is 41.6°.

Series IX.

Control of Series VIII. The individuals were from the same lot as those used in Series VI. They had, however, lived seventeen days longer at 33.5—34°. Two individuals tested.

Nos. 1 and 2. Medium sized; rigor at 43° and 44° respectively; cooled slowly, revived.

The mean, 43.5°, agrees approximately with that obtained in Series V and VI.

Series X.

Control of Series VIII. The lot from which Series III was taken, continued at the same temperature seventeen days longer, having therefore been kept at 15° since hatching. Two individuals tested.

Nos. 1 and 2. Small; heat rigor at 40° and 40.5° respectively; cooled rapidly, both revived, but No. 1 seemed paralyzed on one side; rigor again at 37° and 40.5° respectively; cooled rapidly, No. 2 only revived.

The mean, 40.3°, agrees with the results of Series I to IV.

From these experiments it appears that tadpoles which during thirty-three days in warm water have acquired an increased resistance of 3.2° lose part of that acquired resistance during seventeen days sojourn in cooler water. But the loss is a very slow one. The effect of the high temperature on the tadpoles is not, therefore, transitory, but persists — we have not been able to determine how long — after the cause has been removed.

To recapitulate: Individual organisms have the capacity of becoming adapted to a high degree of temperature, so that a temperature which normally is fatal may be withstood. This adaptation of the individual accompanies the subjection of organisms to temperatures higher than those to which they have already become accustomed. This capacity exists among both Protozoa and Metazoa. The effect of the elevated temperature persists (though in diminished degree) a considerable time after the individual has been restored to a lower temperature.

The facts of individual adaptation to high temperatures are exactly paralleled by similar ones pertaining to density and composition of medium, light, and mechanical stimulus. It is not our purpose to discuss these exhaustively, but we desire to cite a few examples of individual adaptation to changes in these conditions.

It is a familiar experience that crabs taken from the sea may be accustomed to live in water of a density so low that they would have perished if placed immediately in it from sea water. This individual adaptation is effected in accordance with the following rules: 1. The minimum density which will support life lies considerably below the optimum density, or that to which the organism has become adapted; and, 2. the conditions of density under which an individual is living tend to become in time the optimum conditions for that individual. Thus DE VARIGNY ('88, pag. 566) accustomed *Actinia* to live in water consisting of 80 parts fresh and 10 salt water. So EISIG ('87, pag. 798—801) found that the annelid *Capitella capitata* put directly into nearly fresh water, — Sp. Gr. 1.0088 — dies in a few seconds, but by gradually reducing the Sp. Gr. of the water during four months he got individuals to live in water of that density. This adaptation EISIG attributed to the accustoming of the red blood discs of the annelid to fresh water and their acquisition of a capacity for resisting its injurious action, which injurious action is the cause of death when *Capitella* is plunged at once into fresh water. YUNG ('85, pag. 520) found that tadpoles put directly into a 1% solution of sea-salt die in a few hours, but if they are gradually carried up to a solution of that strength through 0.2%, 0.4%, 0.6% and 0.8% solutions, they always adapt themselves to it.

Concerning adaptation to light, VERWORN ('89) has made some important experiments. In the case of the diatom *Navicula brevis*, we have an organism which normally is negatively phototactic, showing no tendency to gather on the illuminated side of the drop of water even when the light is diminished to a scarcely perceptible quantity. A culture kept two weeks in light at the window showed, however, in diffuse daylight a slight, in half darkness a complete aggregation at the positive edge of the drop. In the same way *Stauroneis* also shows plainly that the response of organisms to light is modified by accustoming them to abnormal conditions of illumination.

While experimenting, one of us has made an interesting observation tending to show that individual organisms may become so adapted to an oft repeated mechanical stimulus as no longer to respond to that stimulus. Certain *Stentors* under observation, near the bottom of the aquarium, were constantly struck by some annelids which, half-buried in the mud of the bottom, were waving back

and forth. These Stentors did not contract when struck, as they usually do when touched.

Returning now to our topic of acclimatization of individuals to high temperatures, the question remains to be answered: By virtue of what property can organisms which, like *Flagellata*, normally perish at 25° C., come to live at 70° C., or even higher temperatures?

c) Changes in the Individual Accompanying Increased Resistance to High Temperatures.

What is the nature of the change which protoplasm undergoes in becoming adapted to high temperatures? The most evident change that has occurred in organisms which live at such temperatures as 70° or 80°, is in the point of coagulation of their protoplasm.

As is well known an aqueous solution of ordinary egg albumen coagulates at a temperature below 60°. It was determined, apparently by CHEVREUL (DOYÈRE, '42, pag. 30), that dried albumen, however, coagulates only at a higher temperature, — about 170° C.; and LEWIS ('90) has determined experimentally that the temperature at which coagulation takes place is inversely proportional to the amount of water it contains. This appears from the following table:

Egg Albumen	Coagulation Temperature
in aqueous solution	56° C.
with 25 % water	74—80°
„ 18 % „	80—90°
„ 6 % „	145°
without water	160—170°

Now, coagulation in protoplasm depends upon this property of albumens. If then we have evidence that in cases of high resistance the protoplasm contains less water, we have a sufficient explanation of the fact of the increased resistance. Such evidence we apparently have in many cases.

Thus it has been found that while moist yeast is killed at a temperature below 60°, dry yeast may be heated to 100° C. without losing its vitality (SCHÜTZENBERGER, '79, pag. 162). Damp uredo-spores are killed at 58.5—60° C., but dry ones withstand up to 128° (HOFFMAN, '63); and dry spores of some moulds up to 120° (PASTEUR, '61, p. 81).

According to DALLINGER ('80, pag. 11—14) the dry spores of

various Flagellata are capable of withstanding a temperature from 10° to 27° C. higher than that which these spores can resist in fluid.

According to DOYÈRE ('42, pag. 29) various animalcules (Rotifers, Tardigrades) which cannot withstand in water a temperature of 50° C. may, after long drying, be heated (in air) to 120° C. (rarely to 125°) without all dying.

The foregoing cases show clearly that increased resistance capacity is frequently gained by subjecting the protoplasm of the organism to dryness. But there are other conditions under which the living substance shows extraordinary resistance capacity. In general, as is well known, the spores of organisms withstand higher temperatures than the motile stage, both being in water. This law holds for many cases: —

The spores of some bacteria may be heated for a time above 100° C. without killing them, although their motile stage is killed by 50—52° (LEWITH, '90)

DALLINGER and DRYSDALE ('74, pag. 101), and DALLINGER ('80, pag. 13, 14) have determined maximum temperatures for several Flagellata and their spores in water. While none in the motile stage could withstand a temperature higher than 61°, the spores in water withstood maximum temperatures varying between 65.5° and 131° for the different species.

Have the high resistance capacity of dry protoplasm and that of spores a common cause? Or, in other words, is the protoplasm of spores especially free from water? Many observations make it appear probable that this is so.

Thus in the case of bacteria, the protoplasm of the spore stage is optically denser and occupies less space than in the motile stage (cf. LEWITH, '90).

In the case of the ciliate Infusoria, the larger size of the protoplasmic mass makes the comparison of the condition of the protoplasm in the two stages easier. We glean the facts from BÜTSCHLI ('89, pag. 1652—54). As the process of encystment proceeds, the contractile vacuole continues to function, the intervals between its contractions gradually increase, and finally it disappears some time after the encystment is completed. Hand in hand with these changes goes a gradual condensation of the protoplasm. This condensation BÜTSCHLI believes to be due to an excretion of water from the protoplasm.

In *Actinosphaerium* the change from the richly vacuolated motile form to the encysted condition is even more marked. As BRAUER ('94, pag. 193) has shown, the protoplasmic mass becomes, during the process of encystment, smaller and denser. The loss of water from the protoplasm is without doubt due to the continued activity of the contractile vacuole at a time when no fluids are being taken into the protoplasmic body.

From the foregoing considerations it appears probable that one of the important characters of "spores" is the diminished amount of free water held in the protoplasm; or, in other words, its dryness. This dryness of the coagulable substance would seem to be the cause of its higher resistance.

But herewith not all of the difficulties attending the matter of resistance of organisms to high temperatures are explained. SACHS ('64) insisted that increased dryness of the protoplasm could not be generally adduced as the cause of greater resistance of organisms living in hot water. And indeed, this phenomenon exhibited in the motile stage does offer special difficulties. We know very little concerning the other physiological changes accompanying an increased resistance to high temperatures. It is interesting to note, however, that DALLINGER ('87, pag. 197—198), in his experiments on accustoming *Flagellata* to high temperatures, observed changes in the vacuolization of the organisms accompanying the elevation of temperature. Thus he repeatedly found that after the *Flagellates* had remained at one of the stationary points for some time (see page 234) vacuoles appeared in the protoplasm and then disappeared, and at the same time with their elimination from the protoplasm it gained the capacity of resisting a higher temperature.

It would seem from these observations that even the active organism must get rid of water from the protoplasm before its protoplasm can resist a higher temperature. We are accordingly led to inquire whether the process of acclimatization to higher temperatures may not find its cause in the reduction of the amount of water in the chylema spaces, — the organism becoming in this respect more like a "spore", in which the quantity of free water is reduced to a minimum.

The increased excretion of water from the protoplasm which occurs when the latter is subjected to high temperatures seems to be connected with the increased katabolism accompanying high temperatures. For ROSSBACH ('72) has shown that the rate of

formation of the contractile vacuole in Ciliata increases with the temperature, and in land mammals the excretion of fluids is extraordinarily abundant in hot air.

If, then, organisms become acclimatized to higher temperatures by losing water from their protoplasm, and if the loss of water is a necessary consequence of the increased chemical activity resulting from warmth, it follows that individual acclimatization does occur and must occur as a necessary concomitant of increased temperature.

From this point of view the resistance of organisms living in hot springs is not something to wonder at, but is the necessary result of their environment. How far "adaptation" of organisms to other untoward environments may be explained on chemico-physical grounds does not yet appear.

Cambridge, Mass., Sept. 13, 1894.

Postscript.

Since the above was written, additional evidence that diminution in the amount of the chylema produces increased resistance to high temperatures (page 241) has been gained. Mr. J. I. HAMAKER has at my suggestion gradually acclimatized certain Ciliata to dense solutions, by which operation the body becomes smaller and the protoplasm denser, owing to the fact that water is not imbibed by the protoplasm so readily as in pure water, growth being thus inhibited.

In these Ciliata, as the amount of the chylema is reduced, the point at which heat rigor takes place is elevated.

The experiments of Mr. HAMAKER being still unfinished, further details on this subject must be deferred till the publication of his paper.

C. B. DAVENPORT.

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Zusammenfassung.

Während Protisten gewöhnlich nicht in einer Temperatur von über 60° und Metazoen von über 40° C. leben können, hat man in heißen Quellen Protisten bei wenig unter dem Siedepunkt und Metazoen bei 75° C. lebend gefunden. Diese Widerstandsfähigkeit beruht nicht bloß auf Auslese, sondern es giebt auch eine direkte Anpassung des Individuums an hohe Temperaturen bei langsamer Steigerung derselben. Solche Anpassungsfähigkeit wurde für Protisten und von uns an Metazoen (Kaulquappen) nachgewiesen.

Bei Kaulquappen, welche vom Ei an 28 Tage in Wasser von 25° C. gehalten worden waren, trat die Hitzestarre erst bei 43,5° C. auf, während bei 15° C. gehaltene Quappen schon bei 40,3° C. in Starre geriethen. In 28 Tagen ist also eine vermehrte Widerstandsfähigkeit von 3,2° C. erworben worden und zwar ohne dass eine Auslese durch den Tod von Individuen dabei mitgewirkt hätte. Diese vermehrte Widerstandsfähigkeit geht auch nicht sogleich wieder verloren, denn auf diese Weise acclimatisirte Kaulquappen, welche 17 Tage lang in einer Temperatur von 15° C. gehalten worden waren, geriethen erst bei 41,6° C. in Starre, also immer noch erst bei 1,3° mehr als dem Normalen entsprach.

Der Tod durch hohe Temperatur ist durch Gerinnung des Protoplasma bedingt. Trockenes Protoplasma gerinnt aber noch nicht bei einer Wärme von etwas über 100° C.; daher können eingetrocknete Organismen und solche, die wenig Wasser enthalten, Temperaturen von 100° C. widerstehen.

Der zunehmende Widerstand lebensthätiger Organismen bei langsamer Temperatursteigerung ist daher wahrscheinlich bedingt durch eine Verminderung des Wassergehaltes des Protoplasma, und diese wird durch Zunahme der Abscheidung im Verhältnis zur Aufnahme von Wasser bewirkt. Daher ist hohe Absonderung von Wasser und folglich zunehmender Widerstand gegen Hitze ein nothwendiger physiologischer Begleiter des Aufenthaltes in hohen Temperaturen.

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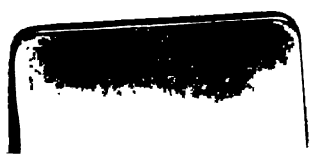
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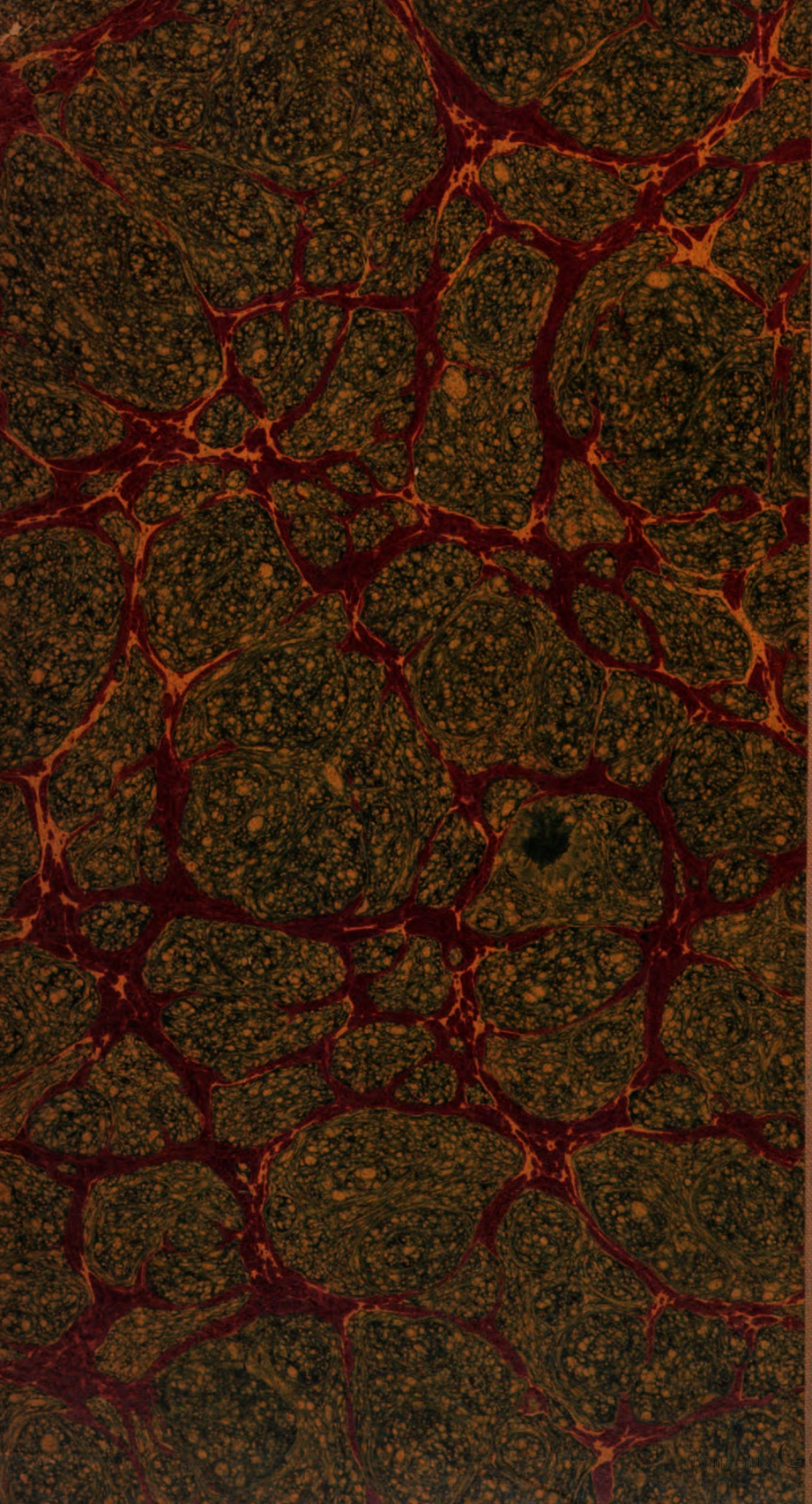
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